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THESIS

THE MORPHOLOGY OF THE LUNGS IN VERTEBRATES

by

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B.S. Smith University, 1931

Submitted in partial fulfillment of the requirements for the degree of Master of Arts

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THE MORPHOLOGY OF THE LUNGS IN VERTEBRATES

INTRODUCTION:

It merely requires a discursive consideration of the literature dealing with subject of the lungs to apprehend at once the many points in question, both anatomically as well as embryologically. Looking at the vertebrate series from fishes to mammals there are few points on which an apparent agreement has been reached by the numerous investigators who have contributed to the field.

Lungs are present in all land vertebrates. They develop from the anterior part of the alimentary canal, and, in most all cases ventrally, except for a few fishes where it is said to take place dorsally. Even, at that, it is by no means certain that this has always been the primitive condition. As expressed by Kerr, the dictates of environmental adaptation would naturally enough tend to force the air-bladder of the fish from a ventral to a dorsal position. In fact, some authors differ as to the early embryonic development of these organs. There are those who claim that lungs are paired evaginations from the posterior portion of the fore-gut. While others hold that the lung-rudiment develops singly and solidly from the pharyngeal region. In the adult condition, however, many varities are seen to exist from the primitive air-sac of Polypterus to complex lungs of mammals.

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Moreover, in searching for a probable origin of lungs in the lower form of vertebrates, the anatomists have long since held that they arose in phylogeny from the air-sacs of fishes. Others who have not accepted the former view, insist that lungs are serially homologous to gill pouches which have extended posteriorly and have taken over a respiratory function secondarily.

As a comparative review of the subject seems desirable in light of the unsatisfactory state of our existing knowledge regarding the morphology of lungs, the author of this thesis has attempted to point out these differences, and, at the same time, bring some of the observations under the rectitude of embryological research.

The function of the lungs in vertebrata has been purposely excluded in the preparation of this thesis. First, because the domains of physiology is for the most part considered separately from morphology, and, secondly, the need of mechanical specialization in order to express its deeper aspects.

PART I

THE ANATOMY OF THE LUNGS

Pisces:

The organ in fishes which is generally considered homologous to the lungs in Tetrapoda is called the air-bladder. It is absent in both Amphioxus and Cyclostomata. In the Elasmobranchii, the sharks and skates, a rudiment of this air-sac still persists in the form of a dorsal diverticulum of the oesophagus, which opens to the pharynx by a duct. Some form of air-sac is to be found in all the Ganoidei and a large majority of the Teleostei. The arrangements of these organs in the Ganoids are much varied. They are always either paired or single sacs. The pneumatic duct connecting the lung vary in length as well as in the point of contact with the alimentary canal. In some cases the opening occurs at the extreme anterior part of the alimentary canal; in others the opening is on the stomach. In Polypterus, a primitive form of air-bladder exist which is paired and opens ventrally to the oesophagus. In Lepidosteus, there is a condition in which the air-bladder is single for the most part on its external surface. The communication with the oesophagus is located on the dorsal wall. The internal surface is transversed by a median longitudinal trabecula making two halves. Each half is again divided into numerous cellular cavities by a series of transverse processes to increase the respiratory surface. A

similar state of affairs has been described for the air-sacs of Amia. It is very highly significant that these variations in the air-bladders of the Ganoids are to be found either in the Teleosts or in higher vertebrates possessing lungs. However, the organ is more lung-like in character owing to the presence of afferent veins and efferent arteries and has hence been regarded as a respiratory organ. In Ceratodus the lung consists of a single sac which occupies almost all the dorsal region between the vertebral column and the alimentary canal. There are paired air-sacs in Protopterus and Lepidosiren. Figure I shows the various forms of air-bladders that have been described. A--of Polypterus bichir (after J. Muller). B--of Johnius Lobatus. C--of Corvina trispinosa (after Cuvier and Valenciennes).

The arteries that supply the air-bladder break up into minute capillary networks known as "retia mirabilia" which form "red spots" on the interior surface. Menge (25) describes the course of the blood as such--"From the retia the blood passes to the postcardinal, hepatic, or vertebral body veins in the Ganoids and Physostomous species, especially those with a wide pneumatic duct." Figure 2 illustrates the course of the blood to Physoclistous * Teleostean air-bladders. Figure 3 illustrates most of the types of air-bladders to be found in fishes. A--Primitive symmetrical arrangement; B--Polypterus; C--Ceratodus; D--Physostomous Teleost; E--Physoclistic Teleost.

** Physoclisti are those Teleost with a closed bladder as

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distinguished from Physostomi fishes with an open duct.
(J. Muller, 1842).

A

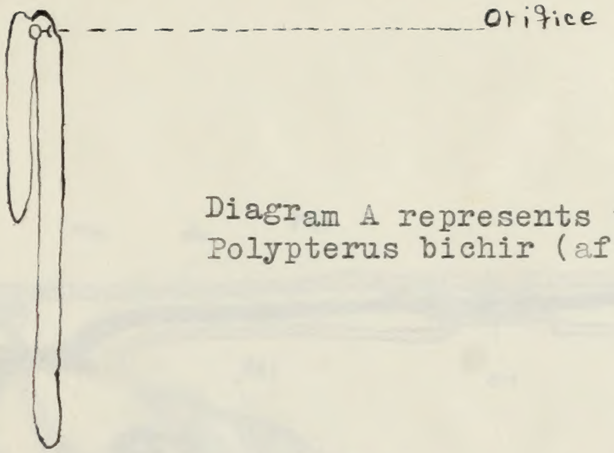


Diagram A represents the air-sacs of Polypterus bichir (after J. Muller)

B

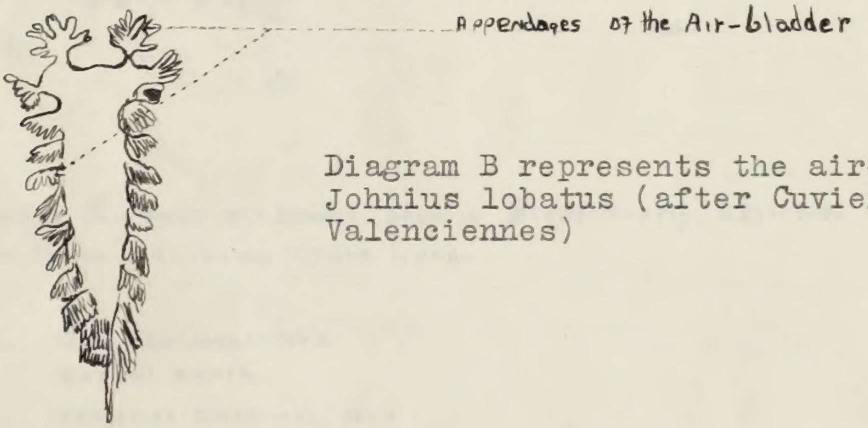


Diagram B represents the air-sacs of Johnius lobatus (after Cuvier and Valenciennes)

C

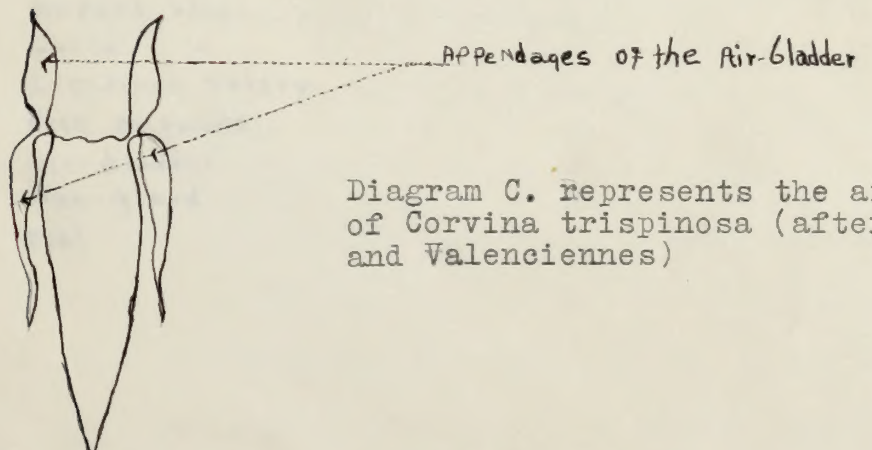
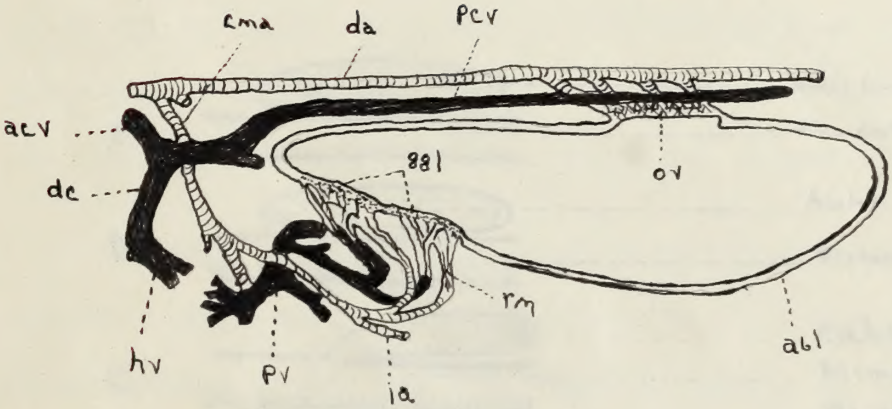


Diagram C. represents the air-sacs of Corvina trispinosa (after Cuvier and Valenciennes)

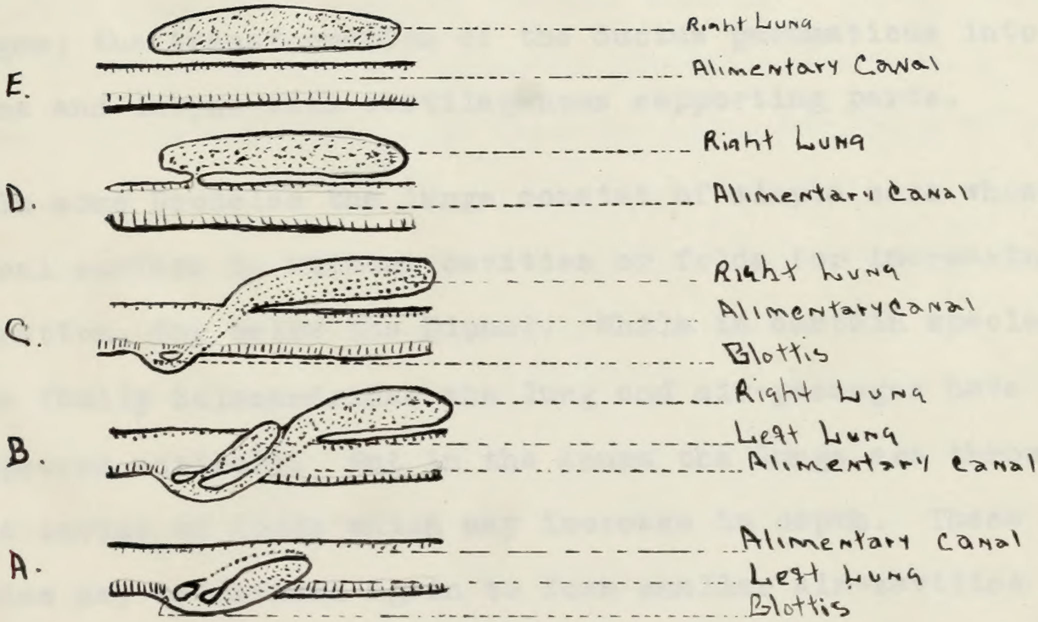
Fig. 1. From Gegenbaur's, Comparative Anatomy, 1878



Physoclistous Teleostean air-bladder Showing Blood-Supply; Left-Side View.
Veins in Black, Arteries Cross-lined.

cma.	Coeliaco-mesenteric
da.	Dorsal Aorta
pcv.	posterior Cardinal Vein
acv.	Anterior " "
dc.	Ductus Cuvieri
hv.	Hepatic Vein
pv.	Portal "
ia.	Intestinal Artery
rm.	Rete mirabile
abl.	Air-bladder
ggl.	Gas-gland
ov.	Oval

Fig. 2. From Goodrich, Structure And Development of Vertebrates, 1930



Diagrams illustrating the various types of air-sacs to be found in fishes.

A--primitive symmetrical arrangement
B--Polypyerus
C--Ceratodus
D--physostomous
E--physoclistic teleost

Fig. 3. From Goodrich, After Kerr, Zoology, 1921

THE ANATOMY OF THE LUNGS

Amphibia:

The lungs of the more highly developed forms of Amphibia have departed but little from the air-bladders of Dipnoi, probably the most pronounced differentiation being in the air passages; the transformation of the ductus pneumaticus into a trachea and larynx with cartilagenous supporting parts.

In some Urodeles the lungs consist of simple sacs whose internal surface is without cavities or folds for increasing respiration, far below the Dipnoi. While in certain species of the family Salamandridae the lung and air-passages have disappeared entirely. But in the Anura the lungs are thrown into a series of folds which may increase in depth. These cavities may be divided again to form smaller air-cavities which are supplied with capillaries from the pulmonary artery. Fig. 4 and 5 are diagrams illustrating the simple saccular condition of the lungs in Urodela and in Anura.

The lungs of some Salamanders are quite asymmetrical; the right being the larger in size. In the Anura, the lungs are oval in shape and attain a greater degree of symmetry. Ballantyne, ('27) in her paper "Air-Bladder and Lungs" describing the Amphibian lungs, states that the lungs of Proteus remain at a lower stage of development than the Dipnoi, in as much as their internal surface is smooth. In some Salamanders and Gymnophiona, the right and left lungs

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are unequal in size, the right being fully developed and transversed by trabeculae.

The Anurans possess typical lungs. In the family Ranidae, the two lungs are distinct, the walls being characterized by series of sacs, or infundibula lined with alveoli. The infundibula open into a median central chamber. Since, this chamber is ciliated and has numerous glands in its wall a good many of writers have held that the cilia are comparable to bronchioli.

A remarkable departure in the respiratory apparatus is seen in the case of those terrestrial urodeles which are lungless in all stages of development. Even after the gills are absorbed, there are no traces of the larynx or trachea. In such species, the respiratory function has been transferred to the skin and the walls of the mouth where a considerable development of capillaries carry out the function of cutaneous respiration.

The air ducts enter the lungs at its anterior end in all amphibians. Whereas, in all other higher vertebrates the lungs extend anteriorly to the entrance of the bronchi on the medial side.

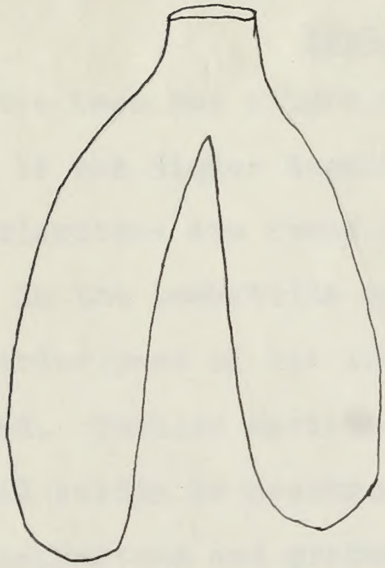

Fig. 4 A diagram of the primitive saccular condition of lower amphibian lungs

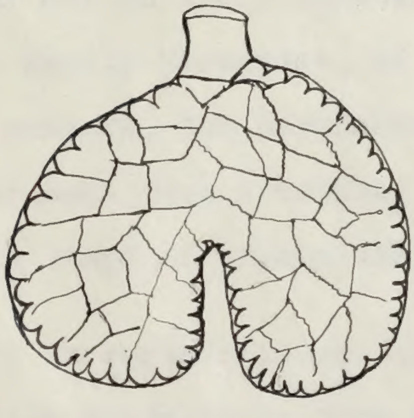

Fig. 5 Diagram showing the cavities and the symmetrical arrangement of the lungs of Anura.

THE ANATOMY OF THE LUNGS

Reptilia:

There have been but slight divergiences in the structure of the lungs of the higher Amphibian and the lower reptile. Striking similarities are found in the saccular enlargements of each group. In the Lacertilia and Ophidia, lizards and snakes, the more anterior part of the lungs have become more highly differentiated. Tubular cavities lead out at intervals from a median central cavity or mesobronchus. This portion of the lung is parenchymatous and gradually comes to a point where the distal portion is a spacious sac as in Anura. Due to the great elongation of the body in snakes, the left lung is vestigial if not entirely absent.

In the family Varanidae, of which the turtles and crocodiles are members, the parenchyme is more highly developed. Secondary bronchi from a tubular mesobronchus extend into each cavity. The lungs of Crocodilia are enclosed in a plural sac.

Finally in certain Lacertilia and Chelonia, there are blind sac-like projections from the saccular portion of the lung which extend out around the viscera in anticipation of air-sacs found in birds.

In Figure 6, is a diagram of a longitudinal section through the lung of Lacertilia. Fig. 7, lungs of Chamaeleo monachus, showing these blind sacs in the distal region.

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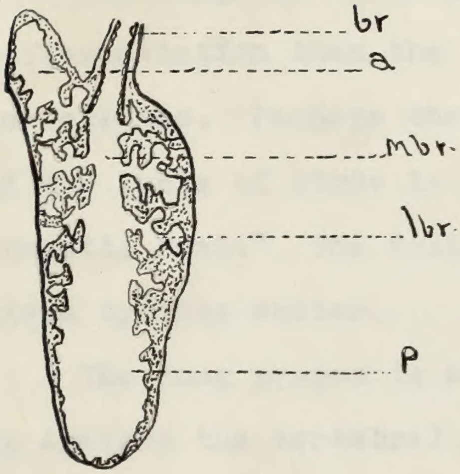
In turtles and crocodiles there are no atria, the lungs

being a very spongy mass. The bronchus in turtles enters on the ventral side of the lung and not medial as in lizards or some other higher forms.

Longitudinal Section of Lacertilian Lungs



br. : Lateral External Bronchus
Mbr. : Main Internal Bronchus
lbr. : Lateral Secondary Bronchus
a : Anterior Extension of Saccular Bronchus.
P. : Posterior Saccular Extension of Bronchus

Fig. 6.

Fig. 6 shows a longitudinal section through the lungs of Lacertilia terminating in a saccular space.

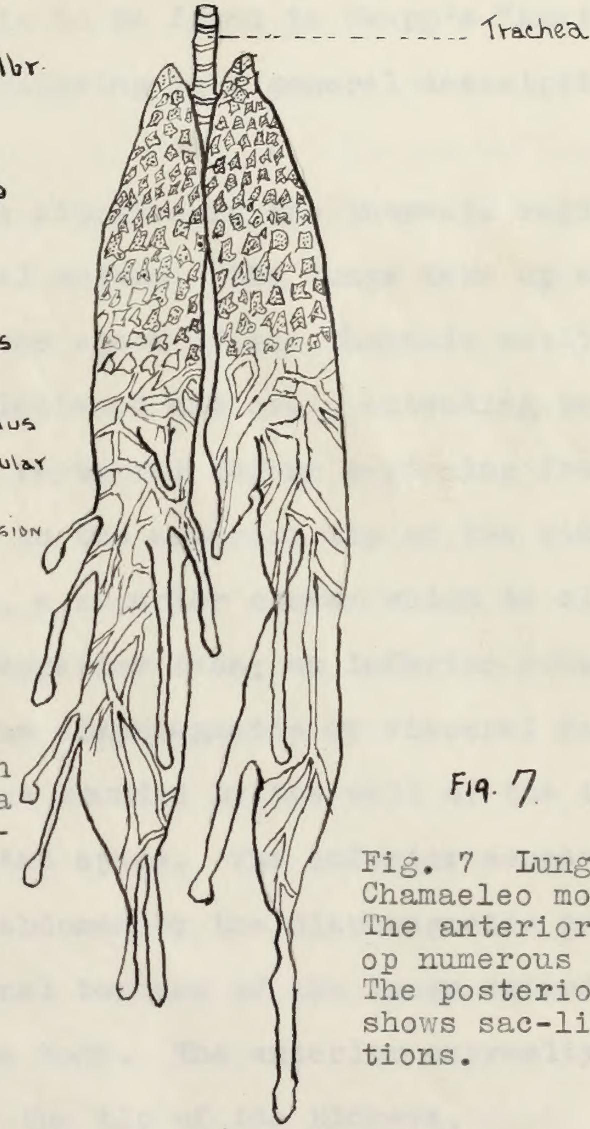


Fig. 7

Fig. 7 Lungs of Chamaeleo monachus. The anterior end develop numerous cavities. The posterior portion shows sac-like projections.

Lungs of Chamaeleo Monachus.

Fig. 6. After Goodrich. Fig. 7. After Wiedersheim

ANATOMY OF THE LUNGS

Aves:

The lungs of birds probably reach a higher degree of differentiation than the lungs of any other group of the vertebrates. Perhaps the most complete account of the anatomy of the lungs of birds is to be found in Kaupp's "Anatomy of the Domestic Fowl." The following is a general description as given by this writer.

The lung proper is situated in the thoracic region, close up against the vertebral column. The lungs take up approximately one-seventh of the space of the thoracic cavity. They are relatively long, flattened and oval, extending posteriorly along each side of the vertebral column beginning from the second dorsal vertebra to the anterior tip of the kidneys. They present two faces, a superior convex which is also called the dorsal costal, or superior face; an inferior concave face which is also called the diaphragmatic or visceral face. The superior convex face bounded by the wall of the thorax and a part of the intercostal space. The inferior concave face is separated from the abdomen by the diaphragmatic partition. The external and internal borders of the lungs extend parallel to the long axis of the body. The anterior extremity is a bit rounded terminating at the tip of the kidneys.

There are two bronchi provided with incomplete cartilaginous rings that enter the lungs at their inferior face, toward the anterior middle. As soon as the bronchi enter the lungs,

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There are two bronchi provided with incomplete cartilaginous rings that enter the lungs at their inferior face, toward the anterior middle. As soon as the bronchi enter the lungs,

the cartilaginous rings disappear; and the bronchi become broadened and divide immediately into primary, secondary, and tertiary tubules at right angles to each other. Fig. 8 is a diagrammatic representation of the air tubules of the lungs, to which Locy and Larsell have applied the names ectobronchi and entobronchi and latrobronchi in the embryo. Also, the recurrent and dorsibronchi can be seen.

Connected to the lungs are five apirs of bladder-like structures, the air-sacs. In fact, by some anatomists these air-sacs have been called "bladder-like, extra-pulmonary expansions of the bronchial tubules free from cartilage." They consist of a minute cellulo-serous membrane receiving their blood supply from the general circulation and not directly from the lungs as has been held by some writers. Situated in the interclavicular space is the interclavicular air-sac. It is usually, Goodrich ('30)," fused to a median sac ventral to the oesophagus in the pectoral region remaining separate in Vultures)". Arising from the lateral walls of the interclavicular air-sac are three prolongations, the subpectoral, the subscapular, and the humeral. A pair of cervical air-sacs which has a number of prolongations supplying the neck vertebrae and the spinal canal. An anterior and posterior pair of thoracic air-sacs which are related to the lungs anteriorly. Finally, two pairs of abdominal air-sacs situated on each side of the abdominal cavity. Like the interclavicular sac, they have a close relation with practically every structure in that region, such as the viscera and the reproductive organs of

both male and female.

All five pairs of air-sacs communicate with bones of their respective location, with the exception of the interclavicular air-sac.

Fig. 9 is a diagram of the general structure and arrangement of air-sacs.

The pulmonary artery of birds arises from the conus arterriosus of the right ventricle. It divides into short, pulmonalis sinister arteries, the shorter one goes to the right, while the longer supplies the left lung. These two arteries divide or branch and follow the course of the bronchi ending in capillary network.

Fig. 9 shows the air-sac of the Fowl in connection with the lungs in the dorsal region.

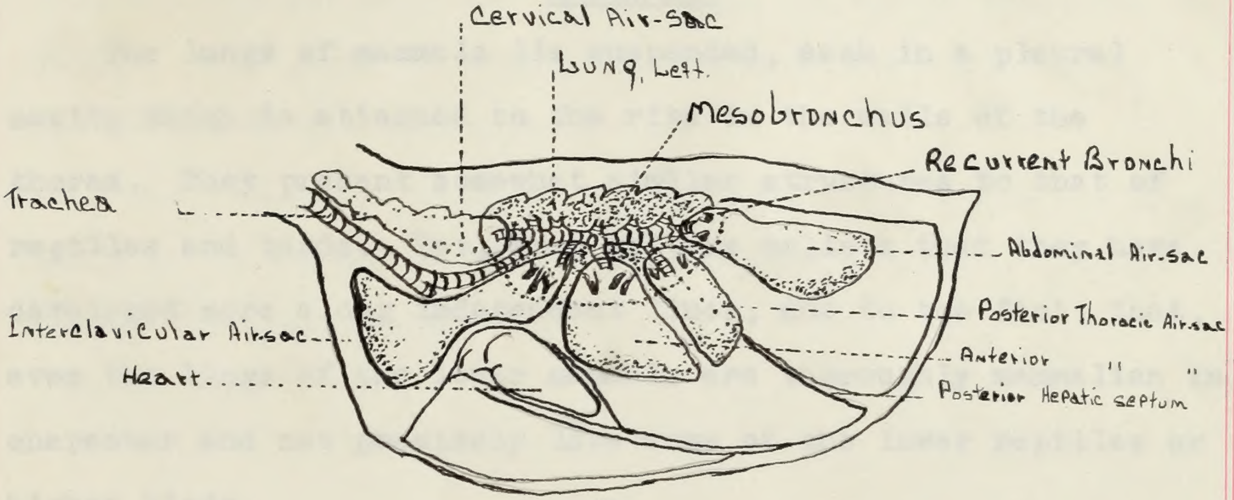

Fig. 9.

Fig. 9 shows the bronchi dividing into ectobronchi, entobronchi, and latrobronchi. Also the recurrent and dorsibronchi can be seen at r and d.

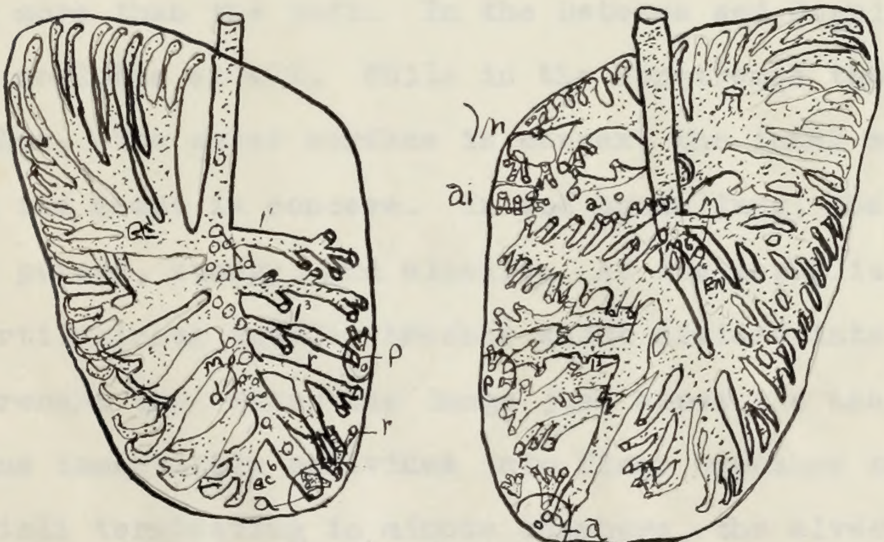

Fig. 8

Lungs of Gallus domesticus

a.: opening of Mesobronchus
mb.: Opening into Abdominal Air-sac
ai.: Region of Recurrent Bronchus from Anterior Intermadiate Air-sac.
ai°.: opening " " " " " "
b.: " " bronchus into " " "
c.: " into Cervical sac; d, Root of Dorsibronchi
ec.: Ectobronchi en. Entobronchi l. Latrobronchi
lm, m.: Openings into Lateral and medial Moieties of Interclavicular sac
p.: " " Posterior Intermediate sac: r. Recurrent Bronchi from Abdominal sac.

Fig. 9. from Goodrich. Fig. 8. from Kingsley After Locy and Larsell,

THE ANATOMY OF THE LUNGS

Mammalia:

The lungs of mammals lie suspended, each in a pleural cavity which is attached to the ribs in the walls of the thorax. They present somewhat similar structures to that of reptiles and birds. Yet, most writers believe that they have developed more along independent lines, due to the fact, that, even the lungs of the lower mammals are thoroughly mammalian in character and not precisely like some of the lower reptiles or higher birds.

Externally, the lung may be divided into lobes, the right having more than the left. In the Cetacea and Ungulata there may be no lobes at all. While in the Monotremes the right only has lobes. The outer surface is convex, the inner surface facing the heart is concave. In the human lung, the tissue is highly porous, spongy, and elastic. At its cephalic end is the cartilaginous tubular trachea which divides into right and left bronchi that enter the lungs just above the heart. The bronchus immediately redivides into finer branches called bronchioli terminating in minute chambers, the alveoli. Fig. 10 and 11 are diagrams of these structures. As the main bronchi give off smaller secondary bronchi, they take three directions, dorsal, lateral, and ventral. Moreover, when the pulmonary artery is in back of the bronchi and secondary bronchi, the bronchi take the name of eparterial bronchi. The reverse of this condition, the term hyparterial has been

applied. The pleura surrounding the lungs is composed of two layers. The one adherent to the lungs is called the visceral pleura, while the one lining the walls of the thorax is designated as the parietal.

The pulmonary arteries, veins, and nerves enter the lung along with, and at the point of the bronchi, and as a rule follow the same course.

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A.

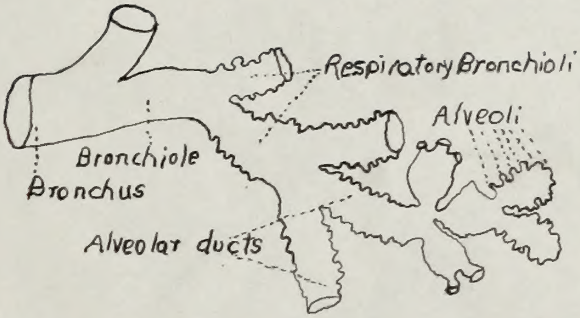


Fig. 10

A, is a diagram of the important structures of the mammalian lung.

B.

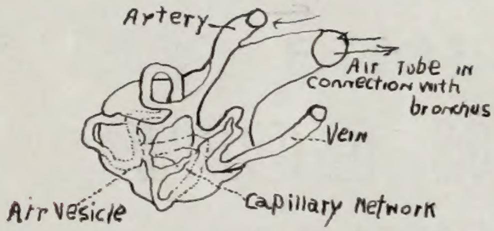


Fig. 11

B, shows the artery and vein ending in capillary network over a thin surface for the exchange of oxygen with the Blood.

A and B from Dakin, Zoology 1927, B. After Johnstone.

PART II

THE EMBRYOLOGY OF THE LUNGS

Pisces:

In spite of the various divergencies in the anatomy of the swim-bladder of fishes, all, develop as diverticula of the wall of the alimentary canal in the approximate region of the gill-clefts. As it arises from this canal it proceeds to grow posteriorly along the dorsal wall of the splanchnocoele. In the physoclistic fishes the duct connecting the alimentary canal becomes constricted losing its connection with this canal. While in the physostomatous fishes, the duct retains its connection. The first appearance of the lung-rudiment is ventral to the alimentary canal but due to rotation (180°) on the part of the lung-rudiment and in part by the alimentary canal itself, the air-bladder eventually develops in a dorsal position as shown in Fig. 12, A and B. In C, is a transverse section from the same species, Rhodeus, showing the lungs as a pouch-like diverticulum of the enteron.

Perhaps the most detailed account of the development of the lungs in the fish has been worked out by Kerr, ('19). Working with the African Lung-fish, he described the development in Ceratodus as an unpaired sac dorsal to the alimentary canal much the same as in the Teleosts, but the ductus pneumaticus opens ventrally instead of dorsally passing around to the right side to the glottis. The general arrangement is

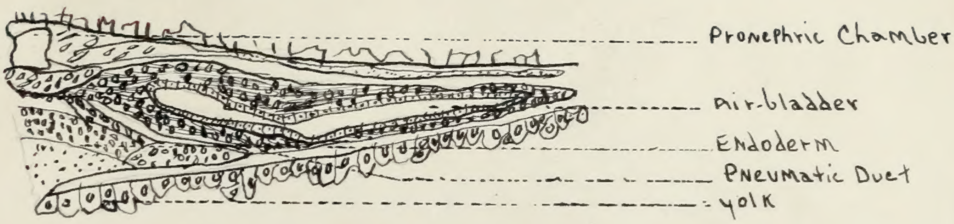
the same in Lepidosiren and Protopterus, except that in these two the organ is found to be deeply bilobed forming a right and a left lung. The lung-rudiment is at first a solid, round, knob-like projection from the floor of the pharynx in the median line. Fig. 13 A, B, and C, show the early stages of the lung-rudiment; stages 32, 34, and 35, of Protopterus; ventral view.

Further, he states, (Kerr) as the lung-rudiment extends tailwards it "twists upon itself in such a way that points upon its ventral surface would move towards the embryo's right side." That is to say, the lung-rudiment rotates in a counter-clockwise direction about its long axis. So that, a complete reversion of position of the lung occurs. Consequently, the right lung, that is, the definitive left, becomes larger and is homologous with the left lung of higher vertebrates. This reversive condition is clearly shown in Fig. 14 which are dissections of the mid-gut of Lepidosiren, stages, 32, 35, 36, and 37, A, B, C, and D, respectively. In the more archaic mode of development, the lung-rudiment, in order to assume its dorsal position describes a spiral path about the oesophagus in such a manner that the hinder portion, which is now bilobed, naturally occupies a place dorsal to the alimentary canal. In Fig. 15 are transverse sections through a Lepidosiren larva (stage 34) to illustrate the changing relations of lung to gut, from a short distance behind the glottis tailwards to a dorsal position." In A, the lung is seen ventral to the alimentary canal, in B, to the right; C, completely dorsal; and in D,

bifurcation commences as it takes a mid-dorsal position.

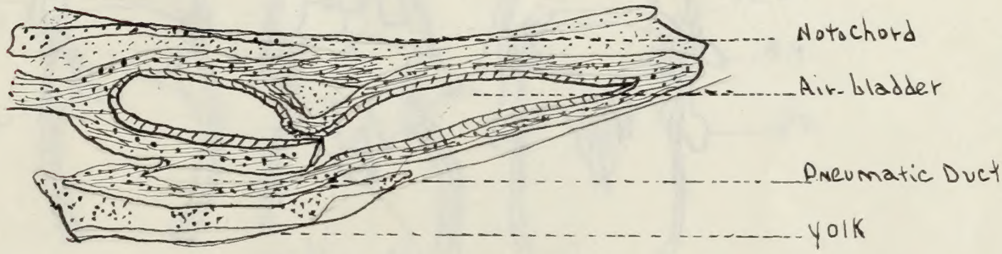
During the early embryonic development of the air-bladder especially in Polypterus and the Dipnoi, paired afferent pulmonary arteries arise in connection with it. These arteries develop from the sixth arterial arch. A pair of "efferent veins return the blood to the hepatic veins near the sinus venosus in Polypterus and directly to the heart in the Dipnoi, where they join to a single pulmonary vein entering on the left side." This fact affords a great deal of evidence in regard to the development of the air-bladder. For, the left pulmonary vessels "Pass round the oesophagus ventrally," just the same as the air-duct to reach the bladder dorsally, which proves that the air-bladder was at one time ventrally placed. Fig. 16 is a diagram showing the relationship between the oesophagus, the pneumatic duct, air-bladder and its blood supply in Prototerus.

A.



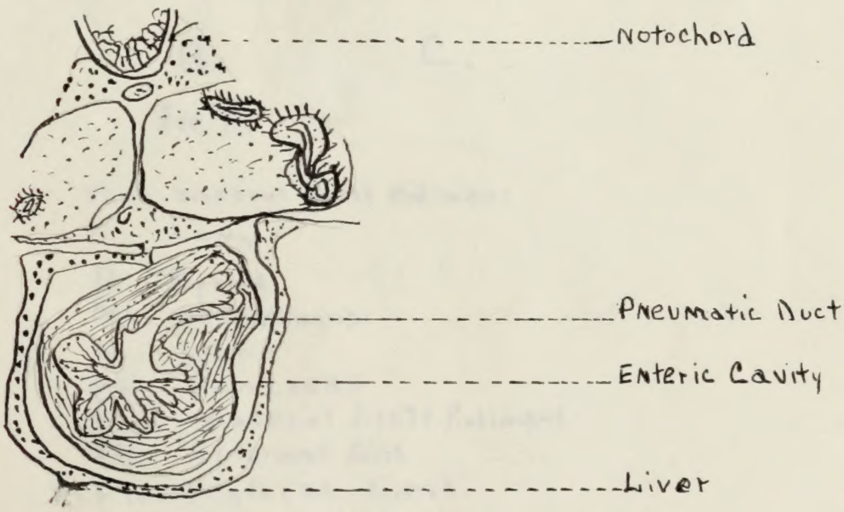
Rhodeus, 5 mm. Longitudinal Section

B.



Rhodeus, 6 mm. Longitudinal Section

C.



Rhodeus, 7 mm. Transverse Section

Fig. 12.

A, B, and C, longitudinal sections, showing the development of lung in fishes.

from Kerr, Embryology of Vertebrata, 1919

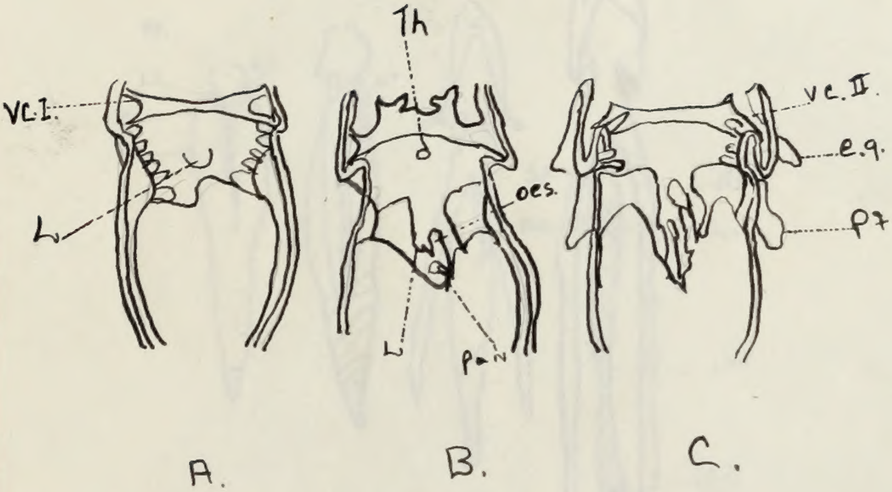


Fig. 13.

Vc.I. Visceral Cleft Rudiment
L. Lung
Th. Thyroid
Oes. Oesophagus
L. Lung
Pan. Pancreas
Vc.II. Visceral Cleft Rudiment
E.g. External Gill
Pf. Pectoral Limb.

A, shows the round, knob-like projection of the lung rudiment. B, bifurcation at the posterior tip; and, C, the paired, lungs extending into the Coelom.

from Kerr, Embryology of Vertebrata, 1919.

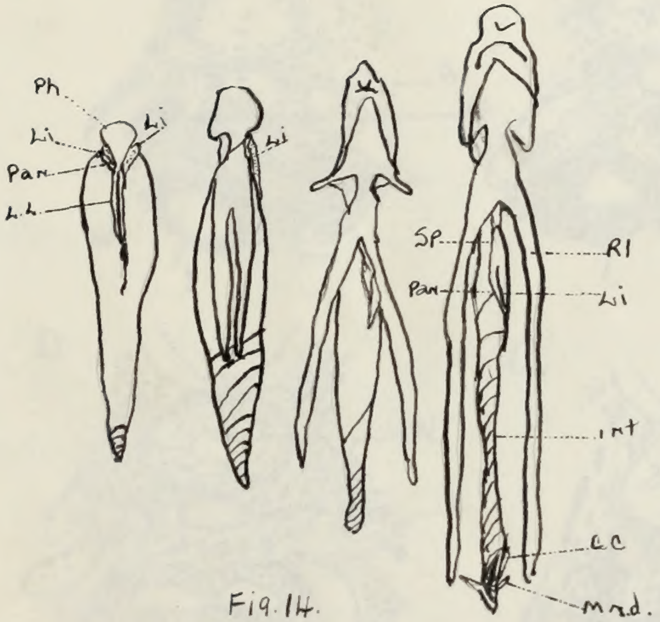
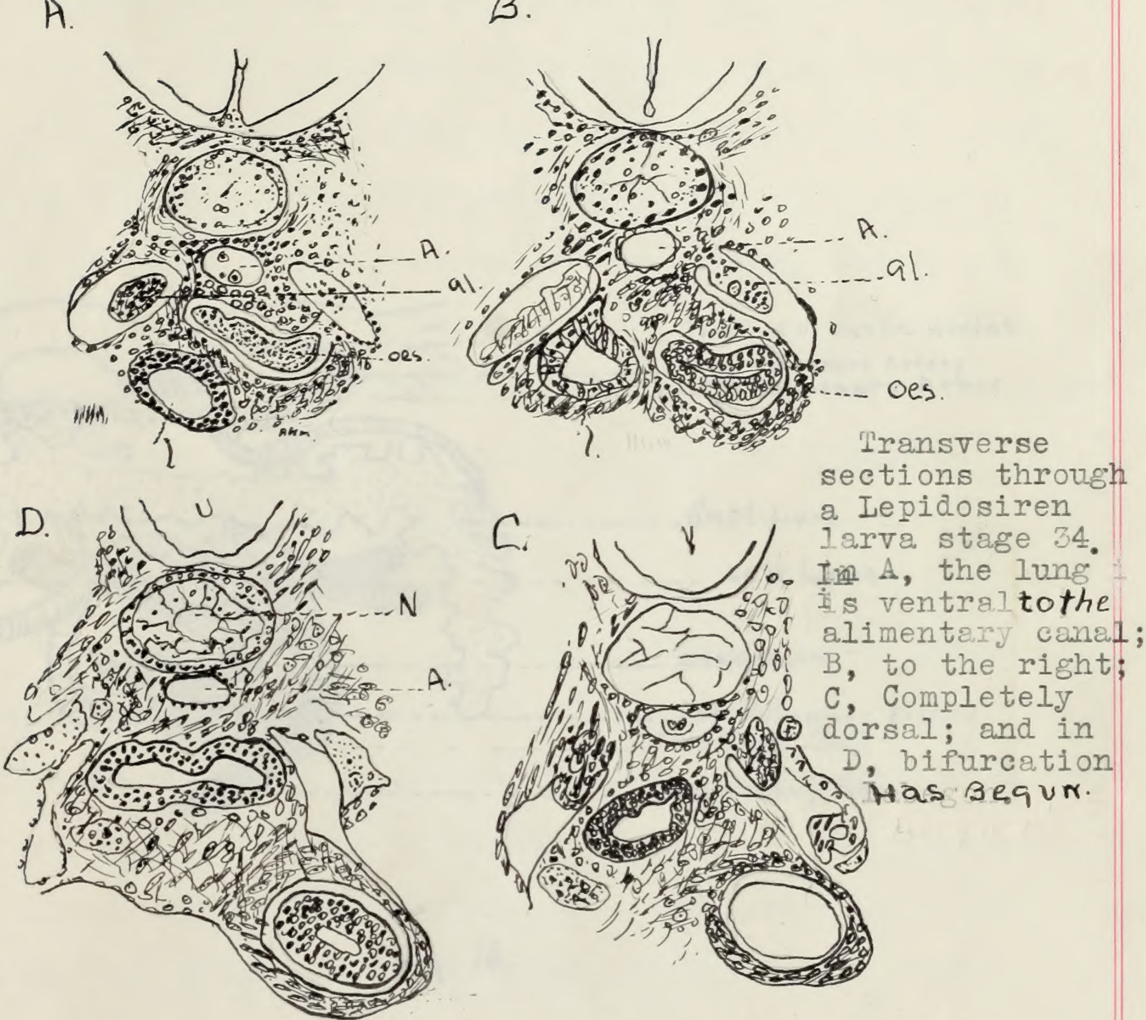


Fig. 14.

Ph. Pharynx
Li. Liver
Pan. pancreas
L.L. Left Lung
Sp. Spleen
R.L. Right Lung
Int. Intestine
C.C. Cloacal Caecum
M.n.d. Wolfian Duct

Diagrams of dissections of the mid-gut of Lepidosiren larva stages 32,35, 36, and 37, showing the rotation of the lung-rudiment.

From Kerr, Embryology of Vertebrata, 1919



Portions of Transverse Sections through A Lepidosiren Larva, stage 34, Showing the migration of the Lung from A ventral position in (A) To A Dorsal position in (D) where it begins to Bifurcate.

A. Aorta
gl. glomerulus of pronephros
L. Lung
N. Notochord
OES. Oesophagus

Fig. 15.

From Kerr, Embryology of Vertebrata. 1919.

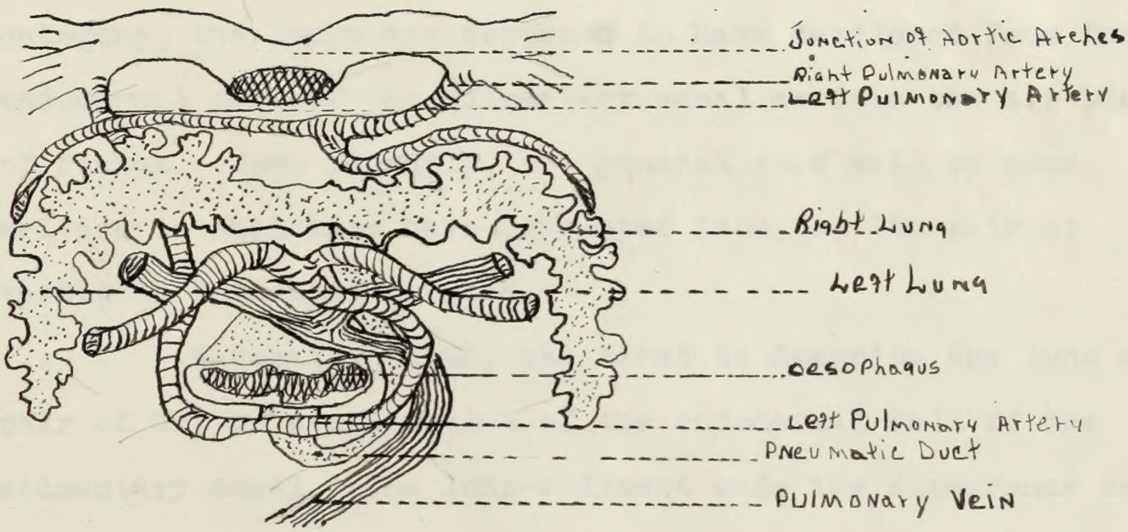


Fig. 16.

A diagram showing the relationship between the oesophagus, the pneumatic duct, air-bladder and its blood supply in Protopterus.

From Goodrich, Vert. Craniata, 1909

EMBRYOLOGY OF THE LUNGS

Amphibia:

The subject of the embryology of the lungs in Amphibia, especially in Anura has commanded a deal of attention during the last 61 years, due largely to their position in the evolutionary history of the respiratory organs. They are the first of the land vertebrates to possess typical lungs. In ontogeny, the lungs are supposed to have developed from the endodermal wall of the alimentary canal as does the air-bladder of fishes. More recently, the general view held by some writers is that they have developed from the 7th pair of vestigial branchial pouches.

Marshall, (1882) was first to describe the lung as a pair of hollow evaginations of the endodermal wall of the alimentary canal. The lung-rudiment made its appearance as two hollow pouches; they were exceedingly small and had pigmented walls. This process of development was supported by later investigators, Morgan, (1897); Reese, ('04); Griel, ('05); Holmes, ('07); Menge, ('25). However, Hempstead, (1900) was far from being in agreement with the previous workers. She holds that the first indication of the lung arises as a solid downgrowth from a solid portion of the pharynx. The lung-rudiment is single and solid, and, that, the lungs sprout laterally from this rudiment. This is still held to be the case in man according to Flint.

Yet, Gotte, (1875) originally described the lungs as being derived from a posterior pair of gill-clefts. Working with Pelobates, he showed that the stages of the lungs are not to be considered as evagination of the fore-gut region, but, rather a transverse widening of branchial pouches. He also held that this was the case in Rana. Weysse, (1895), experimenting with Rana temporaria and Rana esculenta, arrived at the same conclusion.

Recently, much evidence has been brought forward in order to show the origin of lungs from branchial pouches. Makuschok, ('14) and Barrell, ('16) hold that both air-bladders and lungs arise from entodermal pockets of the pharynx which are serially homologous to the pockets which break through to form the gill-clefts. Further, that lungs are branchial pouches and not mere intestinal diverticula is shown in Fig. 18. Fig. 18 is a frontal section of a larva of the mid-wife toad. Axytes;shows the resemblance of the lung-rudiments to gill-clefts. This latter view has been supported by Marcus, ('08, '22), Goodrich ('30), and Noble ('31).

Nevertheless, Edgeworth ('20), discovered that the muscles of the larynx of salamanders were not derived from the branchial muscles, but "arose from the splanchnic layer covering the digestive tract." He, therefore, supported the view held by Griel and others.

The view regarding lungs as endodermal pockets is rather "exceptional for respiratory organs are characteristically ectodermal, that is, derived from the external cellular layer of the body wall," Dakins ('27); in all animals possessing any sort of respiratory organ. However, the latter view seems more plausible if the observations of Marcus, ('08, '22) are correct. He identified 9 visceral arches in the embryo of Hypogeophia, a primitive Amphibian. The first arch forms the cartilage of the jaws, the second arch the hyoid, the third to the seventh the branchial arches, and the eight and ninth, the bulk of the larynx. The entodermal pouch between the hyoid and the jaw bone forms the exterior spiracle. The pouches caudal to the hyoid together with the next four form the gill-clefts. The sixth becomes the ultimobranchial body, an endocrine structure, whereas the pouch lying caudal to sixth gives rise to the lungs.

The mode of development of the lungs in all amphibians proceeds along the same general plan, the differences being but slight in detail according to the particular adaptation the species undergo. However, the description of the process here is for the Anura as given by Marshall, which is in agreement for the most part with the majority of investigators except for a few instances concerning the early formation of the lung-rudiment, whether it is paired or single, or solid or possess cavities in the very early stages.

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After the splitting of the mesoderm and notochord from the entoderm as shown in Fig. 17, the alimentary canal is at the same time being blocked out. It is but one cell in thickness except in the region of the mid-gut, where the yolk-mass is relatively large. The anterior end of the alimentary canal or enteron is called the stomodaeum or mouth and the posterior end the proctodaeum or anus. That portion of the enteron between these two apertures is the mesenteron from which the lungs develop along with the other glandular organs. The mesenteron makes up almost the entire length of the alimentary canal. As the alimentary canal narrows considerably, it constricts mid-laterally, along its longitudinal axis, causing the sides to fold inwardly until they meet. The dorsal tube becomes the oesophagus and the ventral tube the laryngeal chamber. From this wide anterior expansion of the mesenteron, which is also in the region of the pharynx, the "lungs arise as thin-walled lateral outgrowths." This occurs in Rana Temporaria, when the larva is about 8 mm. in length some time after hatching.

The inner walls are lined with splanchnopleure, while the outer layer is of splanchnic mesoderm. The pulmonary arteries appear shortly after hatching as small outgrowths of the upper ends of the efferent arteries which are of the fourth branchial arches. They then extend backwards to connect the lung-rudiments.

The later development of the lung is concerned with increased respiration, which is accomplished by endodermal

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The later development of the lung is concerned with increased respiration, which is accomplished by endodermal

activity being especially marked at certain points along the inner walls forming smaller sacs.

Fig. 24 is a drawing of a transverse section just behind the region of the heart of a 6-7 mm. frog embryo, showing where the lung would appear.

Fig. 25 is a diagram of a section cut posterior to the heart of Rana temporaria some time after hatching, showing the lungs embedded in the surrounding splanchnic mesoderm.

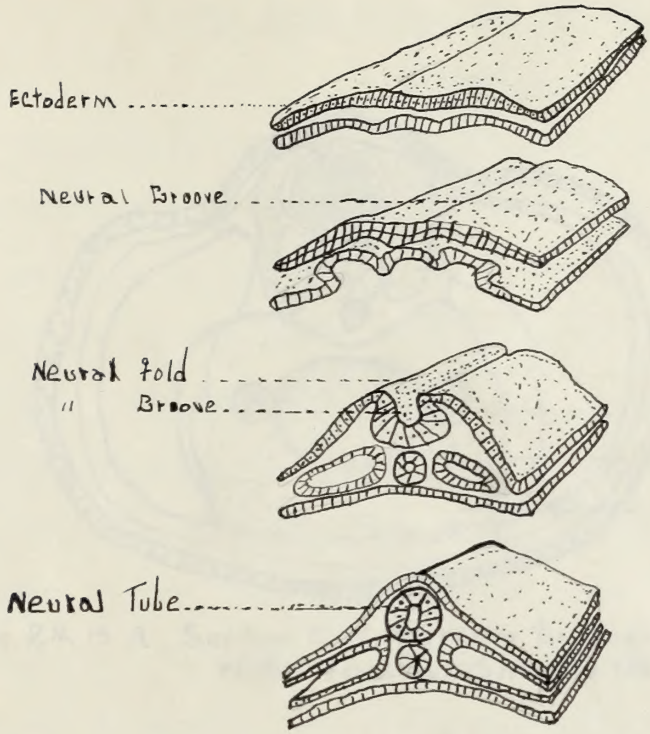


Fig. 17.

Illustrates the separation of the germ layers to form the organs of the body.

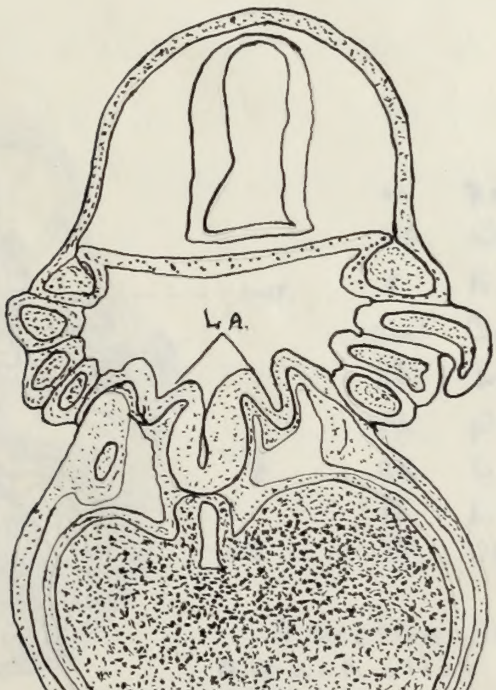


Fig. 18.

A frontal section of Amphibian embryo showing the formation of the lung immediately behind the last formed gill pouch.

L.A. Lung Anlage.

Fig. 17 from Dakin. Fig. 18 from Noble, After Makuschok.

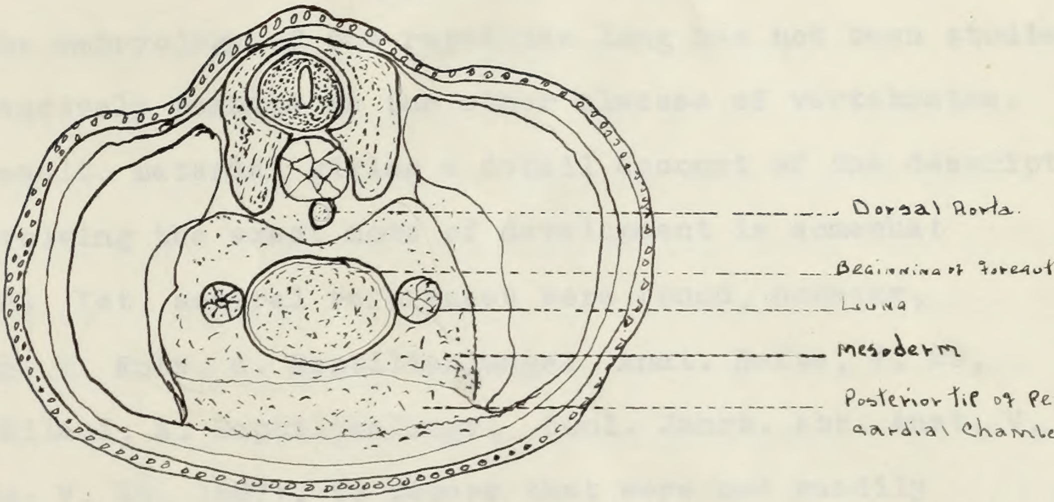
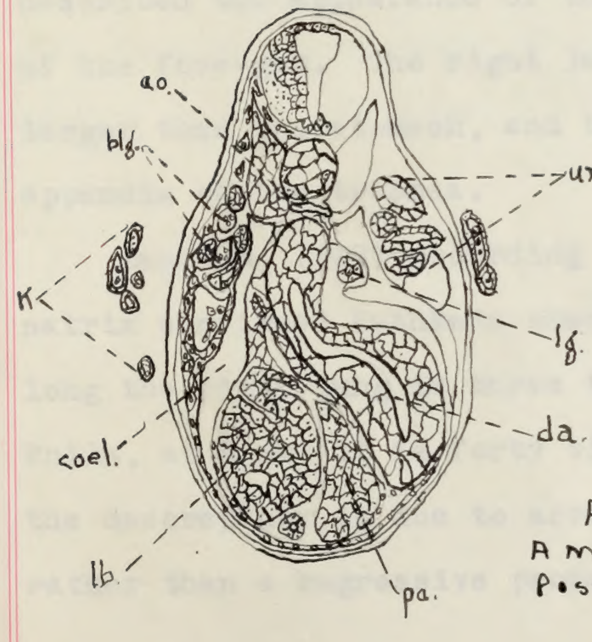


Fig. 24. Is A Section cut Posterior to Heart and at the Beginning of the fore-gut. Showing the Lungs in frog Embryo 6-7mm.



Ao. Aorta
blg. Blutgefäss
K Kiemen
Coel. Coelom
lb. Leberanlage
Pa. Pancreasanlage
da. Darmanlage
lg. Lungenanlage
Ur. Urniere

A Section Posterior to Heart from A much older Embryo Showing the Posterior Portion of the Lung

Fig. 25 After Weysse

THE EMBRYOLOGY OF THE LUNGS

Reptilia:

The embryology of the reptilian lung has not been studied as extensively perhaps as the other classes of vertebrates. As a result, material giving a detail account of the description involving the exact mode of development is somewhat limited. Yet, several references were found, however, (Hesser, K. Entw. d. Reptilienlunge. Anat. Hefte, V. 29, 1905; Milani, A. Reptilienlunge. Zool. Jahrb. Abt. Anat. V. 7, 1894; V. 10, 1897), to papers that were not readily accessible. Consequently, the embryology of the lung will be confined to short references and inferences made by different authors.

Flint, ('06) states that Rathke, studying Coluber natrix described the appearance of the lungs from paired projections of the fore-gut. The right lung increases in size until it is larger than the stomach, and the left remains as a mere appendix of the trachea.

Baumann, ('02) according to Flint, studying Tropidonotus natrix confirmed Rathke's observations that in an embryo 3 mm. long the right lung is three times the length of the left lung. While, at 5 mm. it is forty times larger and concludes that the descrepancy is due to arrested development of the left rather than a regressive process.

While Hesser ('05) as expressed by Goodrich, holds that the subdivision of the lumen of the lung is brought about by outgrowth of successive bud-like branches from a primitive mesobronchus and not by the formation of ingrowing septa. The buds penetrate, sprout, and expand in the surrounding mesoblastic tissue and thus the thicker this layer of mesenchyme the deeper will be the cavities and more developed will be the walls separating them.

The mesenchyme is progressively increased beginning with the lowest reptile up through the highest, so that the primary buds become fewer and more subdivided distally.

It is nevertheless a generally agreement among embryologist that the development of the reptilian lung is quite similar to that of birds.

THE EMBRYOLOGY OF THE LUNGS

Aves:

The embryology of the avain lung has been worked out in great detail and completeness by the researches of a great many embryologists. Consequently the information concerning its development is quite voluminous. Recently, Locy and Larsell ('16) have confirmed as well as elucidated the previous knowledge and studies made by the vast majority of workers. Since this treatment by these two authors is considered to be the latest on the subject, an account of the development of the lungs in the chick will be given as described by them.

"The first appearance of the lung of the chick embryo comes in the early part of the third day as a slight ridge-like enlargement on each side of the latro-ventral surface of the pharynx just behind the fourth gill pouch. So that at the beginning, the primitive lungs are paired, and consist of two shallow pouches that open to the pharynx." The endoderm of the primitive lung give rise to the bronchial tree. The mesoderm of that region supplies the material for the circulatory elements, muscles, and connective tissue; while the ingrowth of ectoderm gives rise to the nerves. At the end of the fourth day, or 96 hours, the lungs have grown considerably dorsally on each side of the oesophagus.

The earliest formation of the bronchial tree arises from the internal cavities of the lung pouches, which are fused

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The earliest formation of the bronchial tree arises from the internal cavities of the lung pouches, which are lined

with endoderm. The endodermal tubes thus formed lie in a layer of mesenchymal cells near the surface towards the pleuro-peritoneal cavity by a mesothelial layer. At the 96-hour stage the endodermal tubes extend into the mesenchyme of the lung primordium, and are slightly exposed at its distal extremities indicating the beginning of the air sacs. During this time the trachea has begun to differentiate from the pharyngo-tracheal groove, and within a few yours it is definitely formed, or established with the lung primordial pouches. The lungs at this stage are quite symmetrical, but, as the ventriculus or stomach develops it pushed on the lung so that it is thrown out of alignment, which gives the appearance of asymmetry. At the proximal end of the lung a short tube lies outside the mesenchymal swelling of the embryonic lung and gives rise to the "extra-pulmonary bronchus."

On the second half of the fifth day of development a spindle-shape expansion arises within the lumen of the endodermal tube. This expansion is the embryonic vestibulum. From this embryonic vestibulum arise the primary, secondary, and tertiary bronchi.

The recurrent bronchi are outgrowths from the air-sacs to complete the circuit of air from the lungs to air-sacs.

At about 52 hours a rounded vascular area occurs in the mesenchyme of the lung primordium, and represents the vascular area of the lung. As to the development of the pulmonary artery it is formed by the union of two parts. The proximal end of the lung receives a sprout from the sixth aortic arch, and a second sprout grows out from the lung wall towards the sprout from the sixth aortic arch. By the union of these two the pulmonary artery is formed sometime during the 75th-87th hours.

According to the observations made by Locy and Larsell, the vascular changes occur before the formation of the sixth aortic arch, which is in disagreement with other workers who hold that the pulmonary artery and vein spring from the sixth aortic arch. However, this latter observation is in agreement with Marshall, (1898) who maintains that the pulmonary arteries arise from the wall of the lung primordium.

Fig. 19 is a reconstruction of the fore-gut of a chick of 72 hours, showing the paired lung-rudiments at the posterior end of the laryngo-tracheal groove.

Fig. 20 is a diagram of the lungs and air-sacs of a chick embryo of about 10 days. The air-sacs are continuations of the original bronchi.

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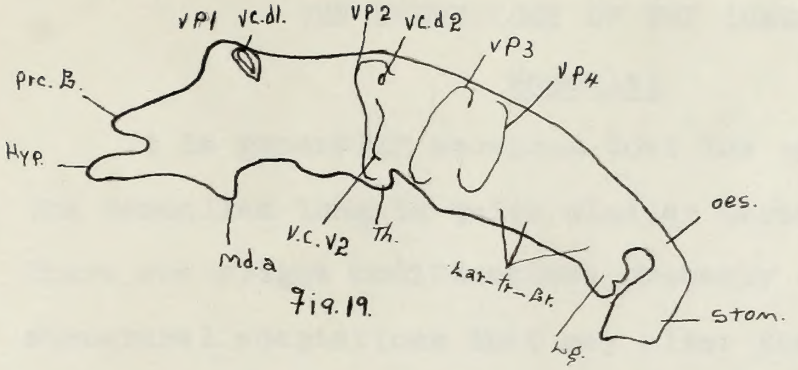

Fig. 19.

Reconstruction of the fore-gut of a chick of 72 hours, showing the paired lung-rudiments at the posterior end of the laryngo-tracheal groove.

Hyp. - Hypophysis. Lar-Tr-Br. - Laryngotracheal Groove. Lg. Lung. Md.a. - Mandibular Arch. - Oes. - Oesophagus. Stom. - Stomach. Pr'o.B. - Preoral Gut. - Th. - Thyroid. - V.c.d. 1.2. - Dorsal Division of the first and Second Visceral Clefts. V.C.V2. - Ventral Division of the Second Visceral Cleft. V.P. 1.2.3.4. first. second. Third and fourth Visceral Pouches.

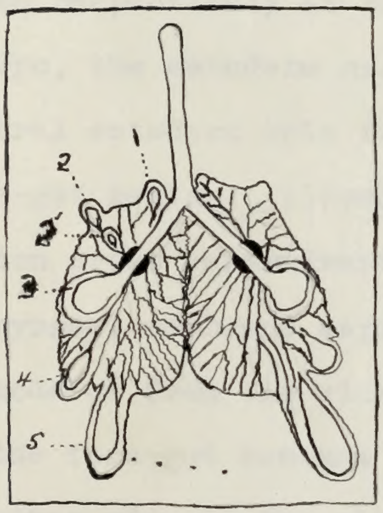

Diagram of lungs and air-sacs of a chick embryo of about 10 days. It shows the air-sacs to be continuations of the original ~~bronchili.~~

Fig. 20.

1. Cervical Air-sac. 2 and 2'. Interclavicular Air-sacs.
3. Anterior Thoracic Air-sac. 4. Posterior Thoracic Airsac.
5. Abdominal Air-sac.

Figures from Lillie, Development of the Chick, After Kastschenko and Selenka.

THE EMBRYOLOGY OF THE LUNGS

Mammals:

It is generally accepted that the early development of the mammalian lung is quite similar throughout the class. There are slight modifications probably due secondarily to structural adaptations that may alter the general plan as initiated. One of the classic examples used to illustrate this process in mammals is the human being. The following account is based upon the description of the process of development as found in Prentis, Text-Book of Embryology, 1915.

After the development of the head and tail-folds, blind endodermal tubes are formed from the vitelline sac, which are known respectively as the fore, mid-and hind-guts. In a 2 mm. embryo, the ectoderm grows so as to come into contact with the ventral ectoderm this forming the pharyngeal membrane of the fore-gut region. Likewise, the ectoderm in the hind-gut region grows ventralwards to form the cloacal membrane. This pharyngeal membrane separates the ectodermal cavity or stomodaeum from the wide anterior portion of the fore-gut. As the fore-gut becomes further differentiated into a pharynx, it gives rise to the pharyngeal pouches, the respiratory organs and other derivatives of that particular region.

In an embryo, about 4 to 5 mm, there are developed 5 pairs of pouches from the lateral wall of the pharynx.

The fifth pair is quite rudimentary. In some lower vertebrates these pouches become to function as gills, but in the Amniota, other structures are derived from them. The first pouch later differentiate into the middle ear and the Eustachian tube. The second is taken up into the pharyngeal wall to form the palatine tonsil. The third, fourth, and fifth give rise to a series of ductless gland, the thymus, the parathyreoids and the ultimo-branchial body, in that order. Meanwhile, there appears a median longitudinal groove on the floor of the pharynx. This groove is the laryngo-tracheal groove and the ridges thus formed on each side are the larynx and trachea. The posterior, rounded end of these ridges is the lung anlage. The lung anlage rapidly increases in size and becomes deeply bilobed when the embryo is 4-5 mm. in length. The lateral furrows become deeper and deeper caudally until a septum is formed separating the respiratory tube from the oesophagus.

As development proceeds when the embryo is 5 mm. the right lung bud grows larger and extend more caudally so that by the time the embryo reaches 7 mm. the stem bronchi give rise to two bronchial buds on the right side and one on the left. The more anterior bud on each side are the apical buds while the others are ventral buds. Thus, there are three embryonic ramifications of the bronchial stem and correspond to the primitive lobes of the lungs.

Prentiss, ('15) states that "on the left side, an apical bud is interpreted as being derived from the first ventral

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Prenties, (115) states that "on the left side, an apical bud is interpreted as being derived from the first ventral

bronchus. It develops later and remains small so that a lobe corresponding to the upper lobe of the right lung is not developed in the left lung (Naroth). The upper lobe of the left lung thus would correspond to the upper middle lobes of the right lung."

The entodermal anlages of the lungs are developed in a mass of mesenchyma dorsal and cranial to the peritoneal cavity. This mesenchymal tissue forms the mediastinum which serves as a support and the surrounding mesenchyma differentiates into cartilage plates of the lung, muscles, and connective tissue.

After the separation of the pleural cavities from the pericardial and the peritoneal cavities, the mesothelium surrounding the lungs becomes the visceral pleura and is derived from splanchnic mesoderm. The layer of tissue outside the pleura lining the walls of the thorax is the parietal and is derived from somatic mesoderm.

As to the development of the air-cells of the lung, they do not begin to form until the sixth month though development is completed during pregnancy (Kolliker).

The pulmonary arteries arise from the sixth pair of aortic arches. In a 11 mm. embryo, they grow lateral and then dorsal to the stem bronchi, the right passing ventral to the apical bronchus. The pulmonary vein receives two branches from each lung.

In Fig. 21 are diagrams of the early development of the

lungs of human embryos (based on reconstructions by Bremer, Broman, Grosser, and Naroth) A, 2.5 mm.; B, 4 mm.; C, inside view of B,; D, 5 mm.; E, 7 mm.

Fig. 22, Dorsal and ventral view of the lungs of a human embryo of five weeks, showing the manner in which embryonic bronchi ramify.

Fig. 23 shows the lungs and pulmonary vessels in a 10.5 mm. embryo.

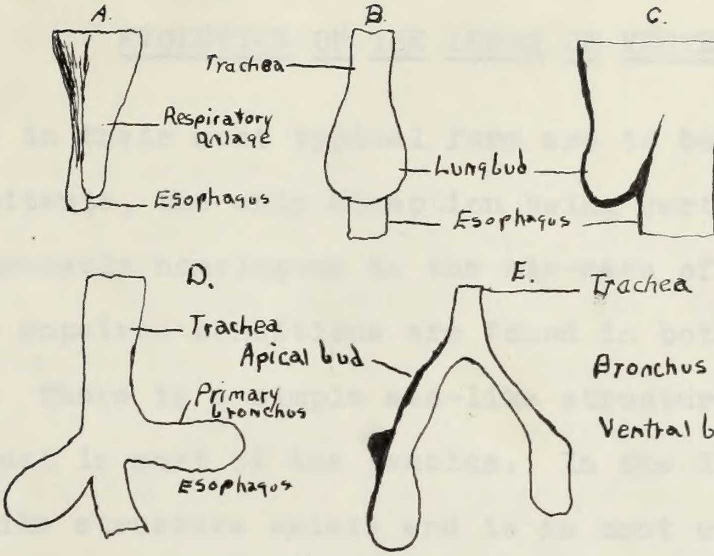
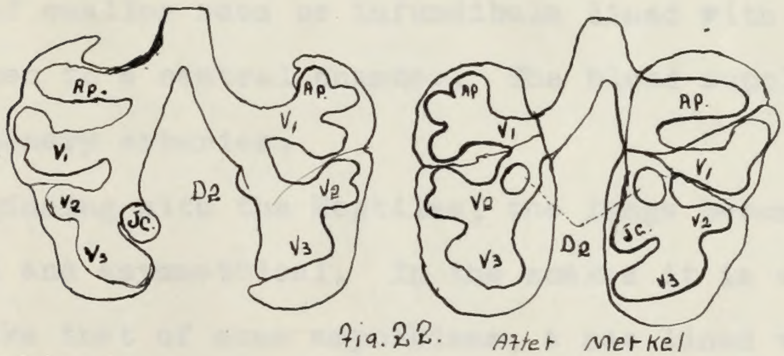


Fig. 21.

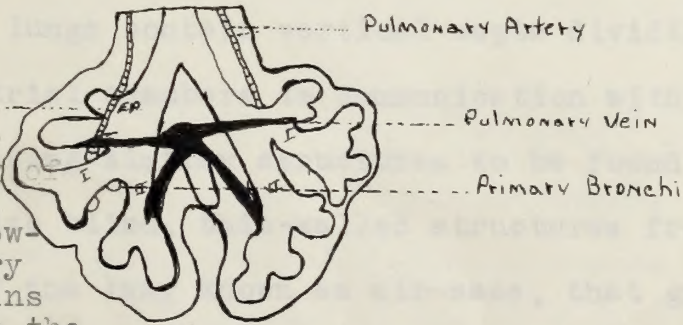
Shows the early development of the lung human embryo.



Is a reconstruction of the lung of a 5-week human embryo showing the primitive lobes and the ramifying bronchi.

Fig. 22. After Merkel

AP. Apical Bronchus; D1, D2; Dorsal Bronchi; V1, V2, V3, Ventral Bronchi; JC. Intracardial Bronchus



Is a reconstruction of the lung of a 10.5 mm. human embryo showing the pulmonary arteries and veins in relation with the lung.

Fig. 23. (His from McMurrich's "Human Body").

Figures from Prentiss, Embryology, 1915

EVOLUTION OF THE LUNGS OF VERTEBRATA:

Lungs in their most typical form are to be found in all land inhabitants, the only exception being certain Urodela. They are probably homologous to the air-sacs of fishes since paired and unpaired conditions are found in both fishes and Tetrapoda. There is a simple sac-like structure connected by a median duct in most of the ganoids. In the dipnoids a typical lung-like structure exists and is in most cases more highly differentiated than those of most Amphibia. In the Anura the lungs are elongated and join at their bases though true bronchi are absent. The walls are divided up into a series of smaller sacs or infundibula lined with alveoli, which open to a central chamber. The blood supply arises from the pulmonary arteries.

Beginning with the Reptiles, the lungs become more complicated and asymmetrical. In the snakes it is a single sac, quite like that of some amphibians, a sac lined with infundibula either in part or throughout its internal surface. In the lizards the lungs contain vertical septa dividing the interior into atrial chambers in communication with the bronchi anticipating similar structures to be found in birds. There develop also blind, thin-walled structures from the posterior end of the lung known as air-sacs, that grow out among the viscera. The turtles and crocodiles do not have

atria, but the lungs are very spongy and are enclosed in virtual pleural cavities.

The birds have gone quite far in the evolutionary development of the lungs. There are two distinct regions one of which is the more parenchymatous vascular portion; the others a saccular area serving as reservoirs. Anterior to the main bronchi at the point where the trachea is continuous, an enlargement appears which is the syrinx or voice box. This structure has no homology among the lower vertebrates, not even the larynx of mammals.

Regarding the relation of mammalian lungs to the lower vertebrates, most workers seem to agree that they have evolved along independent lines. However, in tracing its development, embryologists have turned to the undifferentiated type of amphibian or lower reptilian lung. In so doing two points of view have resulted. One view holds that the lungs are just a further development of the air-bladder of fishes; the other maintains that they are modified branchial pouches, serially homologous to the pharyngeal pockets which break through to form the gill pouches.

The mammalian lung is characterized by great development of a "branching tree-like system of intra-pulmonary bronchi." These ramifying systems of bronchial tubules are strengthened by cartilages present in their walls, and an inner lining of columnar epithelium.

Whether this ramification of the bronchi takes place monopodially or dichotomously is still in doubt. That is to say, in the latter case, by subdivision of the growing tip, in the former, by lateral sprouting from a main stem. Goodrich ('31) supports the view of Moser, which was later confirmed on Reptiles by Hesser. She holds "that the subdivision of the lumen of the lung is brought about in ontogeny, not by the formation of ingrowing septa, but by the outgrowth of successive bud-like branches from a primitive mesobronchus in the lower as well as in the higher forms." To the writer of this thesis, the evidences seem to favor Hesser's view, for, certainly the more primitive the lung, the less parenchyma it contains, and less will be the material for the formation of a great number of cavities and buds as seen in higher vertebrates, where the parenchyme is progressively increased.

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SUMMARY OF THESIS:

In all of the different groups of fishes above the Elasmobranchs there is a single, or paired, air-bladder or, (lung) which is a sac-like diverticulum of the pharyngeal region. It is derived from either the dorsal or ventral sides, and in all cases supplied with blood from the pulmonary arteries.

The pulmonary artery and vein afford conclusive evidence of the fact, that air-bladders and lungs were once ventrally placed on account of the course they take to the left of the oesophagus to reach the dorsally placed air-sacs or lungs.

Structurally the lungs of Amphibia have departed but little from that of most fishes. Even, in the Anura where the lungs attain a higher degree of differentiation internally than in any other members of the class are no more developed than the lungs of the Dipnoi. The greatest difference, however, is one of function, and the controversy over the early stages of development of the lung-rudiment is one of whether it is paired, as it quite probably is, or, whether it is single when it makes its very first appearance in the embryo.

The reptilian lung is characterized by non-symmetry; even one is absent. In the snakes the lung consist of a single sac and is lined with infundibula either in part or throughout.

Whereas, the lungs of lizards are divided by one or more vertical septa. The chambers made by these septa are lined with alveoli, while a portion of the bronchi may extend to the extremity of the lungs.

In the turtles and crocodiles no atria are present and the whole lung is a spongy mass.

The development of these organs are the same as in the birds. Lungs reach their most remarkable development in birds. The lungs are relative large and are connected in the paired air-sacs that extend among the viscera. The trachea divided into bronchi which in turn give off primary, secondary and tertiary bronchi. The recurrent bronchi complete the circuit of air. In development, it has been established that primitively the lungs are paired pouches of the latro-ventral surface of the pharynx just behind the fourth gill pouch. The vascular changes occur in the lung long before the formation of the sixth aortic arch, which is in agreement with Marshall that the pulmonary artery and vein arise from the wall of the lung primordium.

Structurally the mammalian lungs bear close resemblances throughout the class. Even, the Monotremes are thoroughly mammalian. It is believed that this is due to independent lines from which they have developed rather than evolving strictly from higher Aves or lower Reptilia.

Each lung is inclosed in a pleural membrane in the pleural cavity. The lungs are always divided into lobes.

From the main bronchial tube there are dorsal and ventral secondary bronchi; the ventral redivided, and are supported by cartilages present in their walls.

As to the exact mode of development of the amphibian lung it still remains to be worked out, yet, no other view seems to harmonize so well as that the lungs originally came from vestigial branchial pouches.

BIBLIOGRAPHY:

Ballantyne, F. M., 1927 AIR-BLADDER AND LUNGS
Tr. Roy. Soc. Edin., V. 55

Flint, J. M. 1906 DEVELOPMENT OF LUNGS
Am. J. of Anat., V. 6

Hempstead, Marguerite, June 1900 DEVELOPMENT OF THE LUNGS IN THE FROGS; RANA CATESBIANA, RANA SYLVATICA AND RANA VIRESCENS
Proceedings of the Amer. A. A. S., pp. 242-3

Holmes, Samuel, J. 1907 THE BIOLOGY OF THE FROG
pp. 107, The Macmillan C., New York

Huntington, E. S. 1920 PULMONARY EVOLUTION OF MAMMALIA
Am. J. Anat. V. 27

Kerr, J. Graham 1919 TEXT-BOOK OF EMBRYOLOGY
V. II Vertebrata with the exception of Mammalia
Macmillan and Co., London

Kaupp, B. F. 1918 THE ANATOMY OF THE DOMESTIC FOWL
W. B. Saunders Co. Phil. and London
pp. 195-205

Locy, W. A., Larsell, O. 1916 EMBRYOLOGY OF THE BIRDS LUNGS
Pt. I, Am. J. Anat., V. 19
Pt. II Am J. Anat., V. 20

Gegenbaur, Carl 1878 ELEMENTS OF COMPARATIVE ANATOMY
Macmillan and Co., London, pp. 572-3

Marshall, A. Milnes 1882 THE FROG: AN INTRODUCTION TO ANATOMY, HISTOLOGY, AND EMBRYOLOGY Macmillan and Co. London, Eleventh Edition 1920

McEwen, Roberts 1923 VERTEBRATE EMBRYOLOGY pp. 210-16, Henry Holt and Co. New York

Menge, Edward J. 1925 THE STRUCTURE OF THE LUNGS Jour, Morph. V. 27

Morgan, Thomas H. 1897 THE DEVELOPMENT OF THE FROG'S EGGS: AN INTRODUCTION TO EXPERIMENTAL EMBRYOLOGY New York.

Noble, L. Kingsley 1931 THE BIOLOGY OF THE AMPHIBIA pp. 164-8, McGraw-Hill Co., Inc. New York and London

Prentiss, Charles William 1915 A LABORATORY MANUAL AND TEXT-BOOK OF EMBRYOLOGY pp. 173-7, W. B. Saunders Co., Phil. and London.

Weysse, Arthur W. 1895 UBER DIE ERSTEN ANLAGEN DER HAUPTAN-HANGSORGANE DES DARMKANALS BEIM FROSCH, SEPARATABDRUCK AUS DEM ARCHIV FUR MIKROSKOP. ANATOMIE Band XXXXVI, Verlag Von Friedrich Cohen in Bonn

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